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## BIOLOGICAL RELATIONS OF CERTAIN DESERT SHRUBS.

### I. THE CREOSOTE BUSH (*COVILLEA TRIDENTATA*) IN ITS RELATION TO WATER SUPPLY.

V. M. SPALDING.

(WITH SEVEN FIGURES)

THE general features of desert vegetation are well known and have been described in a voluminous literature. Certain striking peculiarities, such as the production of spines, development of tissue for water storage, and particularly the various anatomical means by which the loss of water is prevented or controlled, have received special attention, and still form the usual subject matter of observation and discussion.

These general and easily ascertained facts are by no means unimportant, and it is a decided advantage to botanical science that they have been recorded in such numbers. A far more important fact has become increasingly evident, namely that plants living together under present day desert conditions have each a history and character of its own, expressed in peculiarities of habits and physiological activities, and evidence is not wanting that, with changing and most complicated interrelations of organism and environment, through the long period in which each species has presumably been in the making, these peculiar habits and activities have been acquired.

But apart from all theoretical considerations, it is certain that a fairly intimate knowledge of even a limited number of desert species brings the conviction that no general statement is an adequate expression of the biological relations of any one of them, that each is a law to itself, and that its actual relations to the environment must be determined for each species by critical study of its own structural and physiological characteristics, one by one. It is from this point of view that the present study has been undertaken, and for this purpose certain desert shrubs have been chosen—the creosote bush, palo verde, and mesquite—all of which possess, each in its own way,

remarkable adaptations to desert conditions, and present striking examples of survival in a region that has passed from widely different conditions at an earlier geological period to its present extreme

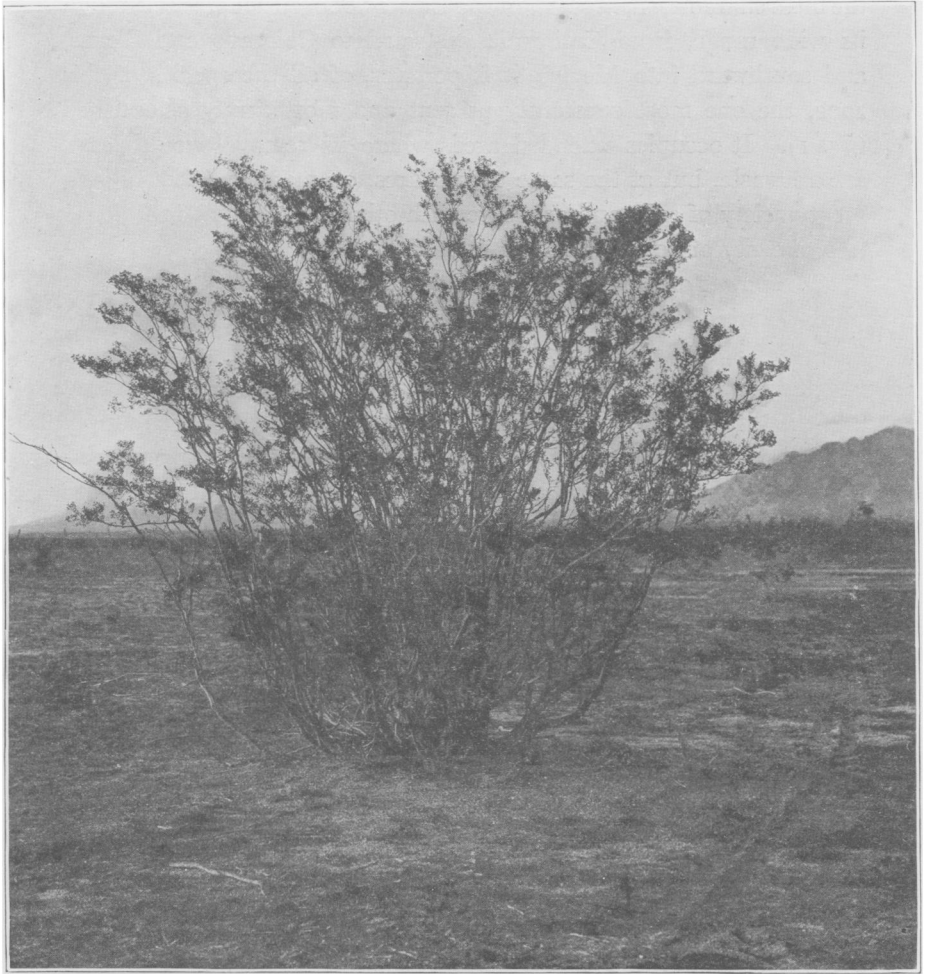


FIG. 1.—*Covillea tridentata*, near Tucson, Arizona.—From Contrib. N. Y. Bot. Gard. No. 46. Plant World 6: pl. 35.

aridity. Work on these several species is now under way at the Desert Laboratory of the Carnegie Institution, and as yet is incomplete. It is thought best, however, to embody in the form of a report

of progress the following notes on the creosote bush and its relations to water supply.

The creosote bush, *Covillea tridentata*, is, as is well known, one of the most characteristic species of the Lower Sonoran zone, and through its wide range, from California eastward to Colorado and Texas, and southward into Mexico, it is perhaps, of all the species of this zone, the one most constantly present and most firmly established (*fig. 1*). It occupies extended areas where its removal would leave a bare waste, but at the same time shares, on mesa and foot-hills, a great variety of soils and exposure with other species that exhibit far less capacity of accommodation than itself.

This power of accommodation is particularly noticeable as regards water supply. One has only to pass from the mesa east of Tucson, for example, to the low ground of the Rillito near Fort Lowell, observing the specimens of creosote bush as he goes along, to be convinced that the differences presented by them are due to the meager supply of water in the one case and its abundance in the other. More striking still are the changes that take place when individual plants are well watered. In contrast with the specimens around them to which no water is given, their leaves become deep green and undergo a marked increase in size, while the whole plant presents the appearance of robust health and remarkable vigor, very different from the pinched specimens with narrow, pale leaves, branches more or less defoliated, and other marks of a struggle that, however successful, is manifestly one of great severity. Plants that have been well watered for a period of years are far more fruitful than their companions standing in dry ground near by, and from their vigor, fruitfulness, and habit of retaining a greater number of healthy leaves and branches, there can be no question as to which is the normal condition; the creosote bush reaches its normal development where there is a full supply of water; arid conditions are indeed tolerated to a remarkable degree, but the plant is dwarfed and suffers in other ways while it endures them (*fig. 2*).

These facts, though matters of every day observation, are highly significant. Provisionally they may be interpreted as indicating that the creosote bush, living over much of the territory where it is now found from the period of maximum precipitation to the present time,

has acquired habits that enable it to withstand excessive drouth, but has never lost its capacity to absorb and use large quantities of water, and attains its best development only under such conditions.

The readiness with which this species accommodates itself to an over-supply of water is shown by a simple experiment. Seedlings of *Covillea* were grown in a flower pot, and after they had made a

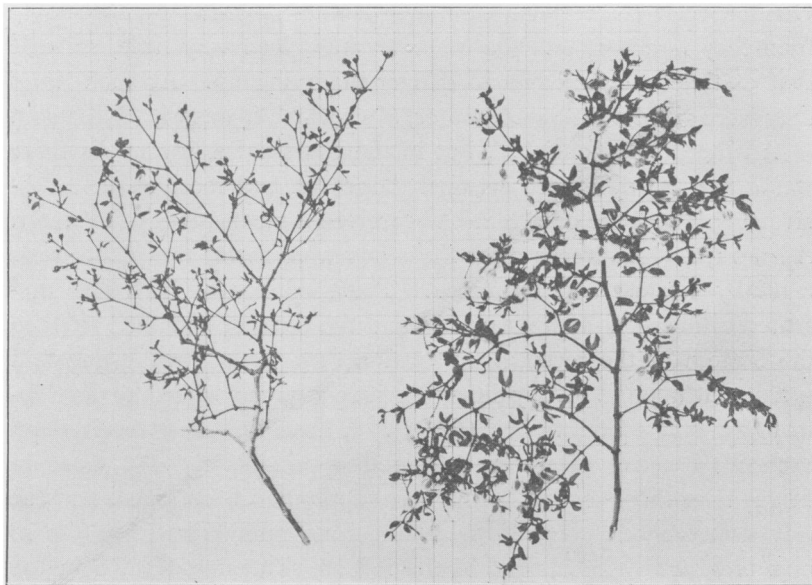


FIG. 2.—Branches of *Covillea*; on the right from a well watered bush near St. Mary's Sanatorium, north of the Desert Laboratory; on the left from the exceedingly dry soil of the mesa close by.

good start were set into a can of water, the bottom of the pot having been broken through in several places. After three or four weeks it was found that some of the roots had grown down into the water and, in contrast with those growing in the soil, had taken the form of water roots, being entirely destitute of root-hairs. The epidermal cells exhibited plasmolysis with a 4 per cent. solution of potassic nitrate, thus indicating their capacity for active absorption. Seedlings grown in the Geneva tester also sent their primary roots down into the water without apparent injury. It is plain, then, that the roots of

Covillea are capable of growing in water, at least for a time, and carrying on normal absorption there.

In order to observe the effects of too great and too small a supply of water on plants growing in soil, seeds were sown in two receptacles measuring  $23^{\text{cm}}$  in depth, and were treated as nearly alike as possible except as to the amount of water given to them. Both stood where they received sunlight through a wire screen during the entire day. One lot received a very large amount of water, manifestly much more than they required, and the other lot was given very little, so little that at times they seemed in danger of drying up. At such times they were given a little more water, after which it was withheld again.

All the plants flourished, but in the course of a few weeks there was a marked difference between those that had received an excessive supply and the ones that had received a meager supply of water. April 12th, eight weeks after the seeds were sown, the plants were carefully washed and examined. The seedlings of both lots presented a fine, healthy appearance, and the roots of both had reached the bottom of the receptacle in which they were growing and had spread out upon it. They differed most conspicuously in the development of stems and leaves (*fig. 3*). Those that had received an excessive amount of water measured approximately  $2^{\text{cm}}$  more in height than those to which a meager supply had been given, and the leaves were both larger and more numerous, numbering from 6 to 10 in representative specimens of the former as against 4 to 8 in the latter; while the largest leaflets in the two lots measured respectively  $1.4$  and  $0.8^{\text{cm}}$  in length. Neither lot showed as strong a development of the root system as plants grown under the same conditions to which an abundant, but not maximum, supply of water had been given. Microscopic examination showed that while both lots were characterized by abundance of root-hairs, these were most numerous and better developed on the roots that had received little water.

It will be instructive to compare with this the record of two other lots of seedlings that had been under observation for a period of seven weeks, during which one lot had been given an oversupply of water, while the other received very little. On March 31st, when they were taken up and washed free from the soil in which they had grown, it was found that the plants to which little water had been given had

a strong and well-developed root system, but that this was very poorly developed in those that had received much water. It was noticeable, too, that while the latter were not altogether destitute of root-hairs, they had not produced them in anything like the abundance characterizing those that had been given little water, there being long stretches on which no root-hairs whatever were to be seen. Both lots of root-hairs showed plasmolysis of epidermal cells near the tip of the fresh root, and of the adjacent root-hairs, with 3 per cent. solution of potassic nitrate, but farther back in both cases plasmolysis was effected with difficulty or not at all. As for the parts above ground, both lots of seedlings had grown well, but those that had been given too much water were of a decidedly lighter green, approaching a sickly color.

From these and other observations it appears that when given an excessive quantity of water seedlings of *Covillea* make a remarkably rapid growth above ground, but produce a less number of root-hairs than those that have a meager supply, besides show-

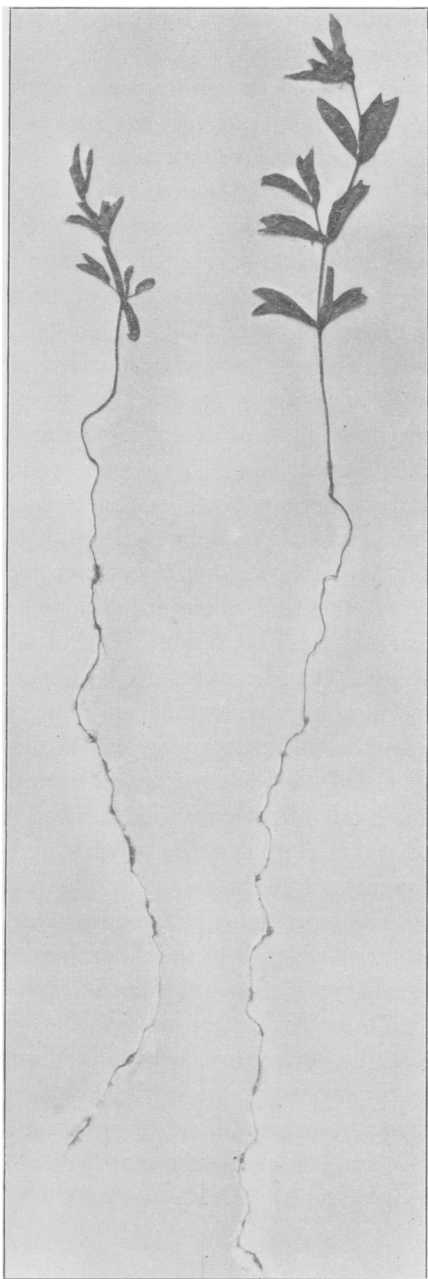


FIG. 3.—Seedlings of *Covillea* eight weeks old, showing effect of excessive and meager water supply.

ing other differences that may be passed over at present. The capital fact, however, is that this species, whether as seedling or mature plant, exhibits an endurance of extremes in the matter of water supply that apparently very few species not possessing a storage system or its equivalent have attained.

This ready adjustment to differences of water supply, manifested not only in power of endurance but also in rate of growth and in other particulars, might naturally be expected to find expression in a corresponding varying rate of transpiration; it becomes, therefore, a matter of special interest to determine the habits of the creosote bush in this respect, particularly after long periods of drouth. Accordingly a series of experiments were conducted in which the hygrometric method of determining transpiration, suggested by Dr. D. T. MACDOUGAL was chiefly employed.<sup>1</sup> By permission of the Desert Laboratory some of the results are here given in advance of publication elsewhere, in which a full account of methods employed by Dr. W. A. CANNON will be given by him.

At the time these experiments were undertaken, late in April, extremely dry conditions, both of atmosphere and soil, had long prevailed. The rainfall since September 1903, a period of nearly seven months, had aggregated only one inch, spring flowers had failed to appear, and during nearly all of the winter and spring an intolerable dust had filled the roads and risen into the air. Under such circumstances it might naturally be expected that transpiration on the part of every plant not artificially watered would be reduced to a minimum; the facts of the case, however, by no means warrant this conclusion.

Two specimens of *Covillea* were selected, one on the hill a little to the northward of the laboratory, the other at the foot of the hill in the same direction. The former presented the fresh appearance exhibited by most of the creosote bushes near the laboratory, indicative of a water supply, however limited, in excess of that in the plain below, where the bushes looked dull and dried-up, as if subjected to most severe conditions, to which it seemed as if they must succumb.

<sup>1</sup>This consists essentially in direct reading of a specially constructed hygrometer placed with the plant under a bell-jar, from which escape of moisture is prevented by oiled silk or a cement base. The correction for vapor-pressure is made once for all by weighing calcium chlorid before and after the saturated air of the bell-jar has been passed through it.

## TRANSPIRATION OF THE CREOSOTE BUSH.

## No. 1. April 22, 1904.

Time A. M.	Percentage of saturation	Temperature	Amount in milligrams
10:51	17	26° C.	105
10:54	19.5	27	121
10:56	22	27.5	149
10:58	25.5	28	177
11:00	29.5	28	198
11:02	35.5	28.5	256
11:04	40.5	29	300
11:06	48	29	355
11:08	54	29	398
11:10	60	29	444
11:12	64	29.5	487
11:14	67.5	29.5	514
11:16	70	29.5	532
11:18	72	29.5	548
11:20	74	29.5	564
11:22	75	30	582

## No. 2. April 23, 1904.

Time A. M.	Percentage of saturation	Temperature	Amount in milligrams
8:57	21	24.5° C.	62
9:03	22.5	25.5	69
9:08	23.5	25.5	72
9:13	24.5	26	76
9:18	26.5	26	84
9:23	29	26	91
9:28	32	26.5	104
9:33	35.5	26.5	116
9:38	39.5	27	132
9:43	42.5	27	142
9:48	46.5	27.5	152
9:53	47.5	27.5	165
9:58	49	28	173
10:03	50	28	178
10:08	49.5	28.5	183

The above table gives in milligrams the aggregate amounts of watery vapor transpired during the indicated periods by each of the plants under observation, and the amounts given off are represented graphically by the accompanying curves (*fig. 4*). The

readings of the hygrometer were reduced by means of the Smithsonian meteorological tables and the appropriate correction then applied for the bell-jar employed. Later experiments indicate that the correction applied in the present case must be considered approximately rather than quantitatively exact, but this does not affect the value of the comparisons that follow.

From the tables here given it is seen that for the time of observation the rate of transpiration of the two plants respectively was: no. 1, 924<sup>mg</sup> per hour; no. 2, 102<sup>mg</sup> per hour.

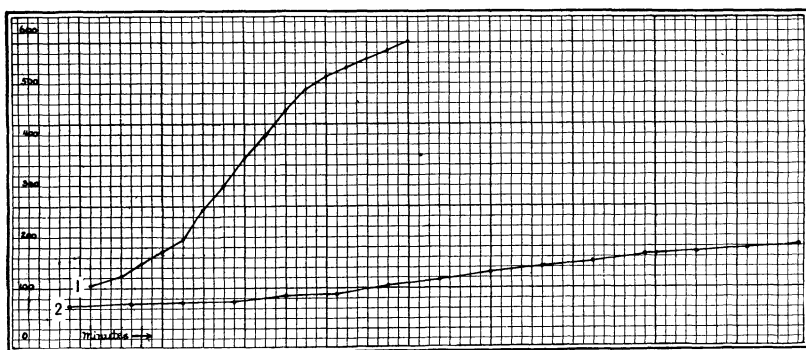


FIG. 4.—Curves showing rate of transpiration of two creosote bushes and amount transpired by no. 1 in 31 minutes and by no. 2 in 1 hour and 11 minutes.

By counting the leaves of each plant and estimating their surface and that of the green shoots on which they were borne, the entire transpiring surface was estimated as: no. 1, 1533<sup>sq cm</sup>; no. 2, 660<sup>sq cm</sup>.

For equivalent surfaces, therefore, the rate of transpiration of no. 1, the plant on the hill, was 3.7 times that of no. 2, the plant on the plain below. Further experiments gave similar results. A branch of a creosote bush growing where the ground had been thoroughly soaked a few weeks before by the running over of water from the tank of the Desert Laboratory was exceptionally fresh and green, and its rate of transpiration, for equivalent surfaces, was found to be 8.9 times as great as that of the bush on the mesa.

From these and other detailed experiments not here reported, it is abundantly proven that after months of excessive drouth the

creosote bush on the mesa and foot-hills is still transpiring considerable quantities of water. The amount transpired appears to stand in direct relation to the amount of water available in the soil where the plant is growing, as is indicated by the following comparison of percentages of moisture given off by the soil when air dried.

Samples of soil were taken at depths of 20 to 30<sup>cm</sup> below the surface from points near the plants on which the transpiration experiments were conducted. In each case the sample was weighed, then left in a shallow basin in the air, exposed to sunlight, but protected from draughts of wind, for three days, after which the weighing was repeated. It was found that the soil from the laboratory hill, taken at a depth of 30<sup>cm</sup> below the surface, lost by air-drying during this period 8 per cent. of its weight, while that from the plain near the foot of the hill, which was much drier and in which the creosote bushes were evidently suffering from lack of water, taken from a depth of 20 to 25<sup>cm</sup>, lost at the same time 3 per cent. Another sample from the hill lost by heating over an electric stove 12 per cent. of its weight. The days when the drying was done the relative humidity of the atmosphere ranged from 20 to 27 per cent.

It is of course essential that much more extended and critical work in this direction should be carried out. Meantime the important fact is established that after months of excessive drouth the soil in which creosote bushes were living, taken only a few inches below the surface, gave up when air dried 3 to 8 per cent. of its weight of watery vapor, while a considerably higher per cent. was driven off by heat. This fact being proven, our interest chiefly centers in the capacity of the plant to utilize the available soil water after it has been so greatly reduced. This involves a study of the root system.

By way of ascertaining first general facts, the roots of creosote bushes were examined by carefully removing the earth in which they were growing, and then following their ramifications as far as possible. This is not an entirely satisfactory procedure, inasmuch as it is quite impracticable to follow the finest roots to the end without breaking them off. It is possible, however, to lay bare so large a part of the root system as to obtain a clear view of its direction of growth, mode of branching, and other characteristic features. *Fig. 5* is a photograph of two seedlings of *Covillea*, a few months old, that

were taken up from the mesa east of Tucson, January 13, 1904. The soil where they were dug, though rather light, is relatively deep,

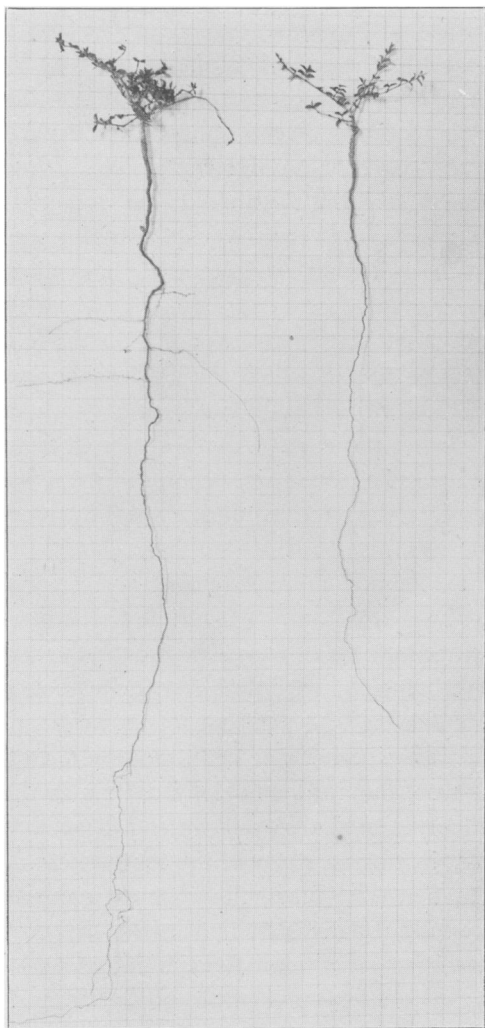


FIG. 5 —Seedlings of *Covillea* from the mesa east of Tucson, Arizona.

and it is noticeable that while the lateral roots had attained only a slight development, the tap-root had reached a depth of over 31<sup>cm</sup> in the one case, and upwards of 53<sup>cm</sup> in the other. A much older plant, taken up from the plain northward of the Desert Laboratory, where the soil is underlaid by rock, shows a strong development of secondary roots, and the tap-root, instead of continuing vertically downward, turns off at a small angle from the horizontal, but finally, at 80<sup>cm</sup> distance from the main axis, turns directly downward. The lateral roots in their turn continue near the surface only a short distance, and then, in spite of the rocky nature of the substratum, turn downwards, reaching 40 to 45<sup>cm</sup> in depth where they were broken off, though probably extending to a considerably greater depth (fig. 6).

The position of this particular plant with respect to those around it is instructive, and may account in part for the distribution of its

roots. Compare the diagram, *fig. 7*, showing the position and distance of a *Parkinsonia*, *Fouquieria*, *Opuntia*, and another *Covillea*. The roots were traced more than half the distance to the *Parkinsonia* in one direction, and to the *Fouquieria* in the other.

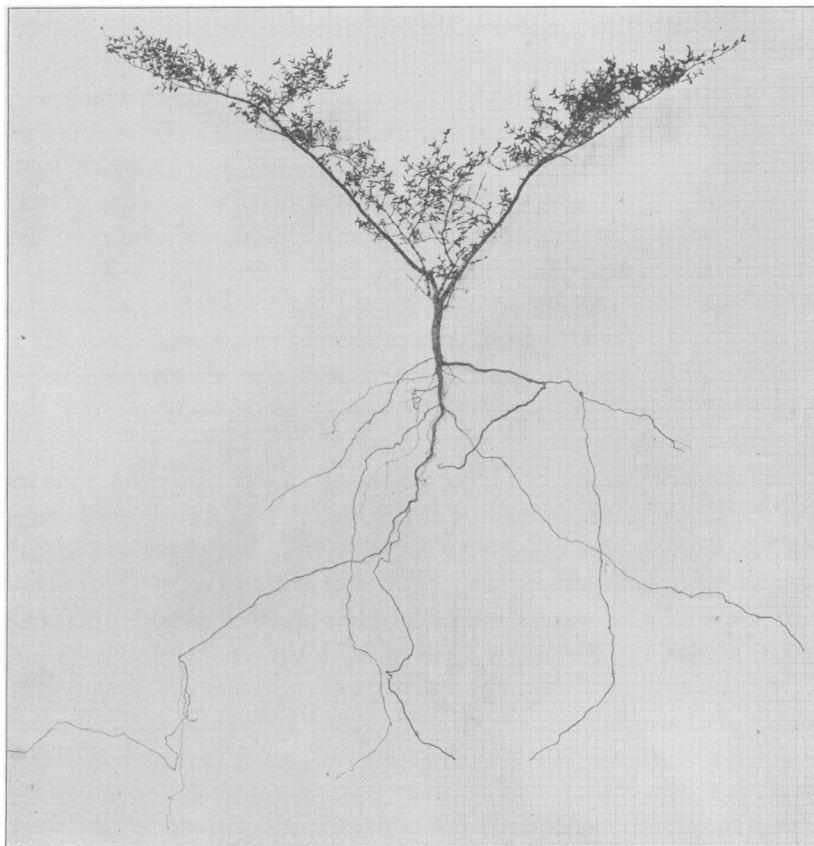


FIG. 6.—*Covillea* from plain to the north of the Desert Laboratory, showing character of root system.

From these and many other individual plants that have been examined, it has been found that the general plan of the root system is essentially the same in all; there is a strong tap-root which grows downwards until it meets an obstruction, or for some other reason changes its course, and slender lateral roots which run near the sur-

face for some distance. It has not thus far been practicable to ascertain the extreme distance to which either the main or lateral roots may extend. At the entrance of an abandoned mine the roots of a rather small plant were found exposed at a depth of 3<sup>m</sup>, and from their size at this point, it is probable that they extended 1.5<sup>m</sup> or more

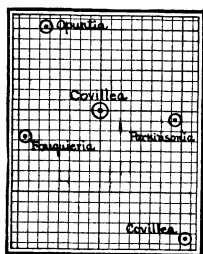


FIG. 7.—Position of *Covillea* with reference to plants around it, on plain north of Desert Laboratory.

farther. Larger specimens doubtless send their roots to much greater distances. In any case it is seen that the root system spreads widely and penetrates deeply into the earth, a disposition well adapted to secure what water is available through a comparatively wide area when there is a light rain, while the longer divisions of the root extend to the water brought by heavier rains that have reached lower levels. Such an arrangement is all the more advantageous in view of the lack of a special storage system, the root as a whole being manifestly incapable of holding any considerable

quantity of water.

The development of the root has been followed for some months by observation of seedlings grown in flower pots and larger receptacles. Some of the results have been referred to already in the discussion of growth of seedlings as affected by water supply. There are other facts, however, particularly the behavior of root-hairs and their relation to absorption, that require separate consideration.

Seeds germinated in a Geneva tester, so that the radicles grew in moist air, gave opportunity to observe the early formation of root-hairs under these special conditions. As was to be expected from what has been observed in other species, they were developed in the damp air of the tester while the radicles were still very short, there being in some instances numerous root-hairs before the radicle had reached a length of 3<sup>mm</sup>. In other cases it had grown to the length of 1<sup>cm</sup>, more or less, before any were produced. In some cases they were close to the root tip, in others farther back, all on one side of the radicle, or projecting from all sides; in short here, where conditions were far more nearly uniform than often happens, there was such variety of habit as to render it extremely difficult to ascertain the factors actually determining the outgrowth of epidermal cells into root-hairs.

Much the same difficulty was experienced with seedlings grown in soil. In some cases the root-hairs arise thickly in complete zones, the rest of the root being free from them; in other cases, while they are abundantly produced, their distribution is extremely irregular; and in still other specimens of the same lot of seedlings the root is nearly naked, there being almost no root-hairs whatever.

In examining a large number of seedlings grown under different conditions other possibly important data in regard to this matter have been obtained, but for our present purpose it is sufficient to emphasize the well established fact that the roots of *Covillea*, whether growing in the lighter soil of the mesa or the heavier soil of the laboratory hill, ordinarily produce great numbers of root-hairs, and that their number becomes less if the plant is given a very large quantity of water. If grown directly in water root-hairs are altogether wanting. Whatever other conditions, then, may or may not afford the stimulus that results in the production of root-hairs in general, the quantity of water in the soil is, in the present case, a factor of prime importance. There is no doubt that the epidermal cells of the root of *Covillea* which would retain their original form if abundantly supplied with water do, as a matter of fact, promptly increase their surface greatly by pushing out root-hairs if the water supply is suitably diminished. Whether in this process the epidermal cell responds directly to the diminished supply of water in the soil around it, or to conditions arising from lack of water in the plant of which it is a part, is a question of theoretical interest well worthy of special investigation.

The epidermal cells near the tip of the root, whether prolonged into root-hairs or not, function as the living agents of absorption. To what extent the older root-hairs may function in the same way, or may serve rather to soak up water like a sponge, when there is an abundant supply, is a question reserved for fuller discussion than can be entered into here. We are now concerned, first of all, with the degree of force with which the undoubtedly vital agents of absorption, the living cells near the root-tip, absorb water from the relatively dry soil in which, as we have seen, the creosote bush maintains itself alive and keeps up its transpiration "stream."

In the investigation of this subject, which is still in progress, seedlings of *Covillea*, of different ages were carefully removed from the

soil and subjected to the action of plasmolyzing agents. A few of the experiments undertaken will be given in detail.

A young seedling, with a slender primary root 2<sup>cm</sup> long, showed distinct plasmolysis of the epidermal cells near the root-tip within five minutes after being placed in 3 per cent. solution of potassic nitrate, and the same phenomenon was soon after obtained as far back as 1.6<sup>cm</sup> from the end of the root. Some of the root-hairs also showed plasmolysis, but not so strongly as the epidermal cells. In the latter it was particularly distinct.

At the same time a number of good specimens growing in the Geneva tester were treated on separate slides with 2, 3, 4, and 5 per cent. solutions of KNO<sub>3</sub> at a temperature of 27° C. With the 2 per cent. solution plasmolysis was not observed; with 3 per cent. it was seen doubtfully or incompletely in a few of the epidermal cells; with 4 per cent. plasmolysis in many epidermal cells was strongly marked; and with 5 per cent. not only was plasmolysis promptly and strongly induced in the epidermal cells but also in some of the root-hairs. It is seen from this experiment, and from others not reported, that the root-hairs plasmolyze less readily than the neighboring epidermal cells. In the present case, while the application of 5 per cent. solution of KNO<sub>3</sub> was promptly followed by plasmolysis of some of the root-hairs, others failed altogether to exhibit the phenomenon.

Similar results were obtained from a lot of seedlings raised in soil in flower pots. They were strong and healthy, and at the end of five weeks' growth, when they were taken up for experimentation, some of them had one or two leaves well developed. Employing the secondary roots of one of the best developed individuals it was found that plasmolysis did not occur in 3 per cent. solution of potassic nitrate; that it took place promptly and distinctly in 5 per cent., both in epidermal cells and root-hairs; and that in 4 per cent. different specimens exhibited a marked difference of behavior. Of five specimens placed in 4 per cent. solution two showed plasmolysis satisfactorily, both of the epidermal cells and root-hairs, while two failed to do so, and one showed plasmolysis well in the epidermal cells but not in the root-hairs.

In these, as generally in roots subsequently examined, it was found that the older root-hairs, farther back from the tip of the root,

are very slow to become plasmolyzed, or for the most part fail altogether, in solutions that readily induce plasmolysis of fresh young cells and root-hairs near the tip. It was found, however, that some of the older root-hairs that are not too far back from the tip exhibited plasmolysis distinctly in a 10 per cent. solution of  $\text{KNO}_3$ , but the great majority are not affected by this nor by higher percentages.

In the course of the work it was repeatedly noticed that many of the older root-hairs presented the appearance of having undergone regeneration, the distal end being clear or semitransparent, in contrast with the dark-colored basal part with its old-looking granular contents, the clear terminal portion being irregular in outline and not infrequently branched. In the course of experiments on an herbaceous plant, *Verbena ciliata*, which showed the same phenomenon even more strikingly than did the creosote bush, it was found that regeneration of its root-hairs could be induced readily by supplying with water a plant from which it had been withheld for some time. It is probable that this capacity for renewed growth on the part of cells apparently dormant may be an important factor in the absorption of water from the soil.

To sum up briefly the observed facts regarding the absorbing cells of the roots of *Covillea*: Root-hairs are, as a rule, produced in large numbers, thus increasing many times the absorbing surface. If the plant receives large quantities of water the number of root-hairs falls off, and when the roots grow in water none are produced, the creosote bush agreeing in this respect with what has been observed in land plants generally. The undoubtedly active absorbing tissue consists of epidermal cells and root-hairs very near the growing point of both primary and secondary roots. These cells fail to show plasmolysis with less than 3 per cent. solution of  $\text{KNO}_3$  and are readily plasmolyzed with higher percentages; their osmotic pressure may accordingly be set down, with more or less variation, as equivalent to ten atmospheres.

The behavior of older epidermal cells and root-hairs is such as to throw doubt upon their functional activity as absorbing cells, though from their observed habit of regeneration under certain circumstances, and from their action with plasmolyzing agents, there are

grounds for assuming provisionally that a considerable proportion of these are still capable of serving this purpose. If they are thus active, their osmotic force, as measured by plasmolysis, is several times that of the younger cells nearer the root-tip. It is apparent, in any case, that the osmotic force exhibited by the root hairs and epidermal cells that are indubitably active is amply sufficient to account for the capacity of this plant to absorb water from the soils in the vicinity of the Desert Laboratory, even after such periods of drouth as those of the present year. Their absorption, however, is necessarily limited by the amount of water available. This, as we have seen, is also a determining factor of transpiration. The means by which the latter is controlled will be discussed elsewhere.

That the creosote bush is able, through its absorbing cells, to abstract continuously a certain amount of water, however small, from such dry soil as that of the desert mesa, to maintain transpiration through many months of excessive drouth, and at the same time to regulate nicely the amount of transpiration to correspond with available water supply, while all the time it is capable of living and does live as an ordinary mesophyte when given a suitable supply of water, is a remarkable fact. Its explanation involves more perfect knowledge not only of the physiological habits now under investigation, but also of the geographical history of the species, which still remains to be written. It need hardly be said that the data for both are to be sought first of all in the desert where this plant is at home.

I desire to express my sincere thanks to Dr. W. A. Cannon, the resident investigator of the Desert Laboratory, and to Messrs. Coville and MacDougal of the Advisory Board for the admirable facilities that have freely been placed at my disposal.

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